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Artículo Original

GEOGRAPHIC AND SEXUAL DIFFERENTIATION OF *Ozotoceros bezoarticus* AND *Subulo gouazoubira* FROM URUGUAY: AN OSTEOMETRIC ANALYSIS OF AXIAL AND GIRDLE SKELETONS

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ABSTRACT. Two native deer inhabit Uruguay: the pampas deer (*Ozotoceros bezoarticus*) and the gray brocket deer (*Subulo gouazoubira*). These taxa are morphologically similar in shape and size, but there is limited knowledge about their anatomy and osteological morphology. Accurate taxonomic identification is crucial for zooarchaeological and paleontological inferences. To assess these issues, we analyzed adult individuals of both sexes from northern and southern regions of Uruguay, focusing on part of the postcranial skeleton: atlas, axis, scapula, pelvis, and sacrum. Twenty-seven measurements were analyzed using univariate and multivariate methods. Variables included species, sex, and geographic origin. The main results show postcranial discrimination between both subspecies of *O. bezoarticus*, corroborating previously observed cranial differences. Also, southern subspecies of pampas deer exhibit larger bones than their northern counterparts. In *S. gouazoubira*, there are clear differences between northern and southern populations, with northern individuals being larger, contrasting with the geographic size patterns in pampas deer. Some postcranial elements of both taxa show sexual dimorphism. However, some bones in which a priori sexual dimorphism would be expected do not show this feature. This work improves the osteological knowledge of these two extant deer and will be useful for solving taxonomic identification (at generic and specific levels) and sex determination challenges in zooarchaeological and paleontological contexts.

RESUMEN. DIFERENCIACIÓN GEOGRÁFICA Y SEXUAL EN *Ozotoceros bezoarticus* Y *Subulo gouazoubira* DE URUGUAY: UN ANÁLISIS OSTEOMÉTRICO DEL ESQUELETO AXIAL Y LAS CINTURAS ESCAPULAR Y PÉLVICA. En Uruguay habitan dos ciervos nativos: el venado de campo (*Ozotoceros bezoarticus*) y el guazubirá (*Subulo gouazoubira*). Si bien estos taxones son similares en forma y tamaño, existe un conocimiento limitado sobre su anatomía y morfología osteológica. Lograr una identificación taxonómica precisa es crucial para las inferencias zooarqueológicas y paleontológicas. Para evaluar estas cuestiones, analizamos individuos adultos de ambos sexos de las regiones norte y sur de Uruguay y nos centramos en parte del esqueleto postcraneal: atlas, axis, escápula, pelvis y sacro. Se analizaron veintisiete mediciones utilizando métodos univariados y multivariados. Las variables incluyeron especie, sexo y origen geográfico. Los principales resultados muestran que existe una diferenciación postcraneal entre ambas subespecies de *O. bezoarticus*, lo que corrobora las diferencias craneales observadas previamente. Además, la subespecie de venado del sur exhibe huesos más grandes que su contraparte del norte. En *S. gouazoubira*, existen claras diferencias entre las poblaciones del norte y del sur, los individuos del norte tienen mayor tamaño,

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lo que contrasta con los patrones geográficos de tamaño observado en los venados. Ambos taxones muestran dimorfismo sexual en algunos elementos postcraneales. Sin embargo, algunos huesos en los que *a priori* se esperaría observar dimorfismo sexual no muestran esta característica. Este trabajo mejora el conocimiento osteológico de estos dos ciervos actuales y será útil para resolver los desafíos de identificación taxonómica (a nivel de género y especie) y determinación del sexo en contextos zooarqueológicos y paleontológicos.

Key words: Pampas deer, gray brocket deer, South America, sexual dimorphism, principal component analysis.

Palabras clave: Venado de campo, guazubirá, América del Sur, dimorfismo sexual, análisis de componentes principales.

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INTRODUCTION

Deer have been present in the South American fossil record since the Early Pleistocene (Webb 2000). In Uruguay, fossil deer comprises four species, characterized by large palmate antlers: *Antifer ultra* Ameghino 1889, *Morenelaphus brachyceros* Gervais & Ameghino 1880, *Morenelaphus lujanensis* Ameghino 1888, and *Paraceros fragilis* Ameghino 1888 (Ubilla et al. 2016), that became extinct at the end of the Pleistocene (Cassini et al. 2016). The primary factors contributing to the extinction of megafauna, including these deer, are believed to be global climatic changes at the end of the Pleistocene, along with the arrival of humans on the continent (Cione et al. 2003; Barnosky & Lindsey 2010; Araujo et al. 2017; Prates & Perez 2021).

Currently, two native deer species remain in Uruguay: the pampas deer (*Ozotoceros bezoarticus* Linnaeus 1758) and the gray brocket deer (*Subulo gouazoubira* Fischer 1814). The pampas deer once inhabited open grassy areas from the southern Amazon to the northern tip of Patagonia and from the pre-Andean regions to the Atlantic coast (Cabrera 1943; González et al. 2002). However, habitat fragmentation has led to isolated populations across their historical range (González et al. 2010). In Uruguay, two distinct subspecies inhabit different regions: *O. b. arerunguaensis* in the north (*El Tapado*, Arerunguá, Department of Salto) and *O. b. uruguayensis* in the southeast (*Los Ajos*, Department of Rocha) (González et al. 2002).

In contrast, the gray brocket deer inhabits a range stretching from southern Uruguay to northeastern Brazil, primarily in closed environments, avoiding very open or heavily wooded areas (Mannise et al. 2019). Formerly classified within the genus *Mazama* Rafinesque 1817, the gray brocket deer coexisted sympatrically with other *Mazama* species in South America. However, recent phylogenetic studies revealed that *Mazama* is polyphyletic (Gilbert et al. 2006; Duarte et al. 2008; Gutiérrez et al. 2017; Heckeberg 2020). Following a taxonomic revision, the gray brocket deer was reclassified into the monospecific genus *Subulo*, previously named *Subulo simplicicornis* Smith 1827, now named *Subulo gouazoubira* (Bernegossi et al. 2022).

Fossil and archaeological records of Uruguay include the pampas deer and gray brocket deer (Moreno et al. 2016; Ubilla et al. 2016). Zooarchaeological evidence indicates that ancient human populations exploited all three Neotropical deer taxa present in this region (*Ozotoceros*, *Subulo*, and *Blastocerus*) although the pampas deer likely experienced the most intensive use (Moreno 2016; Moreno et al. 2016).

While cranio-mandibular studies have received more attention (see Vezzosi & Chimento 2021), few studies have focused on postcranial variability in extant and fossil taxa. Most of these works address interspecific variability (e.g., Lister 1996; Jacobson 2003; Breda 2005; Curran 2015; Loponte et al. 2019; Mucciolo 2019). Studying postcranial elements is particularly valuable for estimating body mass in living and extinct species, which is essential for autoecological and synecological studies, as body mass is closely linked to many life history parameters (Rotti et al. 2021).

Morphological identification of isolated postcranial elements in the fossil record is critical. This is especially true in zooarchaeological contexts, where remains are often fragmented, and multiple taxa may be present at the same site. Some studies have carried out morphometric analyses of isolated and fragmented remains of postcranial elements of deer in archaeological contexts. For example, Castaños et al.

(2014) analyzed the scapula and humerus of *Rangifer* and *Cervus* to identify osteometric criteria that could improve their differentiation. Likewise, osteometric studies have been carried out on *Blastoceros* to make a sexual classification of zooarchaeological remains in the lower Paraná (Mucciolo 2019). As well as the study of sex ratios and hunting strategies for reindeer in Europe (Weinstock 2000). However, it should be noted that no multivariate analysis of the data was carried out in these works.

Accurate taxonomic identification is thus essential to better understand how past human populations utilized different species. A notable challenge in this area is exemplified by Moreno et al. (2016), who analyzed ancient DNA from zooarchaeological remains initially identified as pampas deer *Ozotoceros bezoarticus*. However, DNA analysis revealed these remains were from gray brocket deer *Subulo gouazoubira*. This highlights the difficulties in distinguishing postcranial morphology between species and suggests a potential underestimation of the representation of gray brocket individuals in the archaeological record and, consequently, in studying their role in ancient human diets and management practices. This issue prompted Loponte et al. (2019) to investigate postcranial discrimination between pampas deer and gray brocket deer in specimens from Argentina.

Moreover, there is a wide latitudinal variation in body size within the gray brocket deer population, with individuals from southern regions larger than those from northeastern areas (Silva-Caballero & Ortega 2022). As Moreno et al. (2016) suggested, a size overlap of bones with pampas deer can result in identification errors.

The main objective of our study is to assess and analyze postcranial differences between gray brocket deer and the two pampas deer subspecies that inhabit Uruguay through osteometric methods. Morphological and morphometric differentiation will refine the identification of postcranial archaeological remains and enhance our understanding of their ecological roles and interactions with ancient human populations.

MATERIALS AND METHODS

We surveyed the following osteological collections: Colección Susana González, Instituto de Investigaciones Biológicas Clemente Estable (SG-IIBCE), Montevideo, Uruguay; Museo Nacional de Historia Natural (MNHN), Montevideo, Uruguay; Colección de Vertebrados, Mamíferos, Facultad de Ciencias, Universidad de la República (ZVC-M) Montevideo, Uruguay. Thirty-eight individuals were selected, and 133 elements were measured, including the atlas, axis, shoulder, and pelvic girdles (**Table** 1).

We took 27 measurements following the guidelines of Von Den Driesch (1976) (see **Fig**. 2 for the complete set of measurements used in each bone). All measurements were taken using a vernier caliper (to the nearest tenth of a millimeter). In some elements, we could not obtain the entire set of measurements due to breaks or tissue or joint elements adhering to the bone.

Given the differences in the skull of pampas deer between the northern and southern populations (González et al. 2002), and given that preliminary genetic studies on the gray brocket deer suggest two possible different units recognized in the northern and southeastern areas of the country (González et al. 2020), we have included the geographic provenance as a grouping factor to evaluate differences or variation between individuals from the different regions in both species (**Fig**. 1).

Univariate analysis and principal component analyses (PCA) were performed using the software JMP (JMP®, Version 11.0. SAS Institute Inc., Cary, NC, 1989-2023) and PAST (v.4.11) (Hammer 2001). For the univariate analysis, differences among species, geographical provenance, and sex were assessed using a Student's t-test (Sokal & Rohlf 1995) for each measure of all elements. PCA was conducted using the variance-covariance matrix on untransformed data, disregarding groups. Missing values were addressed through iterative imputation. Subspecies (in the case of *O. bezoarticus*) and regions (in the case of *S. gouazoubira*), as well as sex, were used as grouping factors.

Abbreviations

Atlas: BFcr, greatest breadth of the *facies articularis cranialis* (cranial articular surface); GB, greatest breadth over the wings; GL, greatest length; H, greatest height (**Fig**. 1A).
Axis: BFcr, greatest breadth of the *facies articularis cranialis*; H, greatest height; LAPa, greatest length of the arch including the *processus articularis caudalis*; LCDe, greatest length of the corpus (body) including the dens; LCDe*, greatest length of the corpus without including the dens (**Fig**. 1B).
Scapula: BG, breadth of the glenoid cavity; DHA, diagonal height; GLP, greatest length of the *processus articularis* (glenoid process); HS, height along the spine; Ld, greatest dorsal length; LG, length of the glenoid cavity; SLC, smallest length of the *collum scapulae* (neck of the scapula) (**Fig**. 1C).

Table 1

Specimens analyzed with their corresponding collection number, procedence, and sex assignment.

Species	Code	Procedence	Sex
S. gouazoubira	SG n/n	Rivera	Female
S. gouazoubira	SG1019	Rivera	Male
S. gouazoubira	MNHN 5505	Rivera	Male
S. gouazoubira	MNHN 6434	Rivera. Estancia Los Abuelos	Male
S. gouazoubira	MNHN 8222	Rivera. Cuchilla Negra	Male
S. gouazoubira	ZVCM 1730	Maldonado	Male
S. gouazoubira	MNHN 3068	Lavalleja	Female
S. gouazoubira	MNHN 3167	Lavalleja. Aguas Blancas	Male
S. gouazoubira	MNHN 5507	Lavalleja. Parque Salus	Male
S. gouazoubira	MNHN 7631 (1)	Lavalleja. Parque Salus	Female
S. gouazoubira	MNHN 7631 (2)	Lavalleja. Parque Salus	Female
S. gouazoubira	MNHN 7632	Lavalleja. Parque Salus	Female
O. *b. arerunguaensis*	SG1000	Salto. El Tala	Male
O. b. arerunguaensis	SG1004	Salto. El Tapado	Female
O. b. arerunguaensis	SG1006	Salto. El Tapado	Female
O. b. arerunguaensis	SG1010	Salto. El Tapado	Male
O. b. arerunguaensis	ZVCM 1309	Salto. El Tapado	Male
O. b. arerunguaensis	ZVCM 1310	Salto. El Tapado	Female
O. b. arerunguaensis	ZCVM 1324	Salto. El Tapado	Female
O. b. arerunguaensis	ZVCM 1479	Salto. El Tapado	Female
O. b. arerunguaensis	ZVCM 1614	Salto. El Tapado	Female
O. b. arerunguaensis	ZVCM 1620	Salto. El Tapado	Female
O. b. arerunguaensis	ZVCM 1632	Salto. El Tapado	Male
O. b. arerunguaensis	ZCVM 1753	Salto. El Tapado	Male
O. b. arerunguaensis	ZVCM 5526	Salto. El Tapado	Male
O. b. uruguayensis	SG n/n	Rocha. Los Ajos	Male
O. b. uruguayensis	SG n/n	Rocha	Female
O. b. uruguayensis	SG0019	Rocha. Los Ajos	Male
O. b. uruguayensis	SG0140	Rocha. Los Ajos	Female
O. b. uruguayensis	SG1039	Rocha	Female
O. b. uruguayensis	SG1070	Rocha. Los Ajos	Male
O. b. uruguayensis	SG1088	Rocha. Los Ajos	Female
O. b. uruguayensis	SG1089	Rocha. Los Ajos	Female
O. b. uruguayensis	SG1105	Rocha. Los Ajos	Female
O. b. uruguayensis	ZVCM 1499	Rocha. Los Ajos	Female
O. b. uruguayensis	ZVCM 1590	Rocha. Los Ajos	Female
O. b. uruguayensis	ZVCM 1728	Rocha	Female
O. b. uruguayensis	ZVCM 1735	Rocha. Los Ajos	Female

Pelvis: GL, greatest length of one side; LA, length of the acetabulum including the lip; LAR, length of the acetabulum on the rim; LFo, inner length of the *foramen obturatum*; LS, length of the symphysis; SH, smallest height of the shaft of the ilium (**Fig**. 1D). Sacrum: BFcr, greatest breadth of the *facies terminalis cranialis*; GB, greatest breadth across the wings; GL, greatest length on the ventral side; HFcr, greatest height of the *facies terminalis cranialis*; PL, physiological length (**Fig**. 1E).

RESULTS

Of the 38 individuals analyzed, 26 correspond to *O. bezoarticus* and 12 to *S. gouazoubira* (see **Table** 1). Not all individuals represent complete skeletons; in the case of *O. bezoarticus*, the scapula was the element with the highest number of individuals analyzed (19), while the axis was the element with the lowest number of individuals (11) (**Table** 2). For *S. gouazoubira*, the scapula and the axis were the elements with the highest number of individuals (12 in both). At the same time, the sacrum was the one that presented the lowest number of individuals (8) (see **Table** 2).

Atlas

In the univariate analysis, when comparing the two species (i.e., *O. bezoarticus* and *S. gouazoubira*,

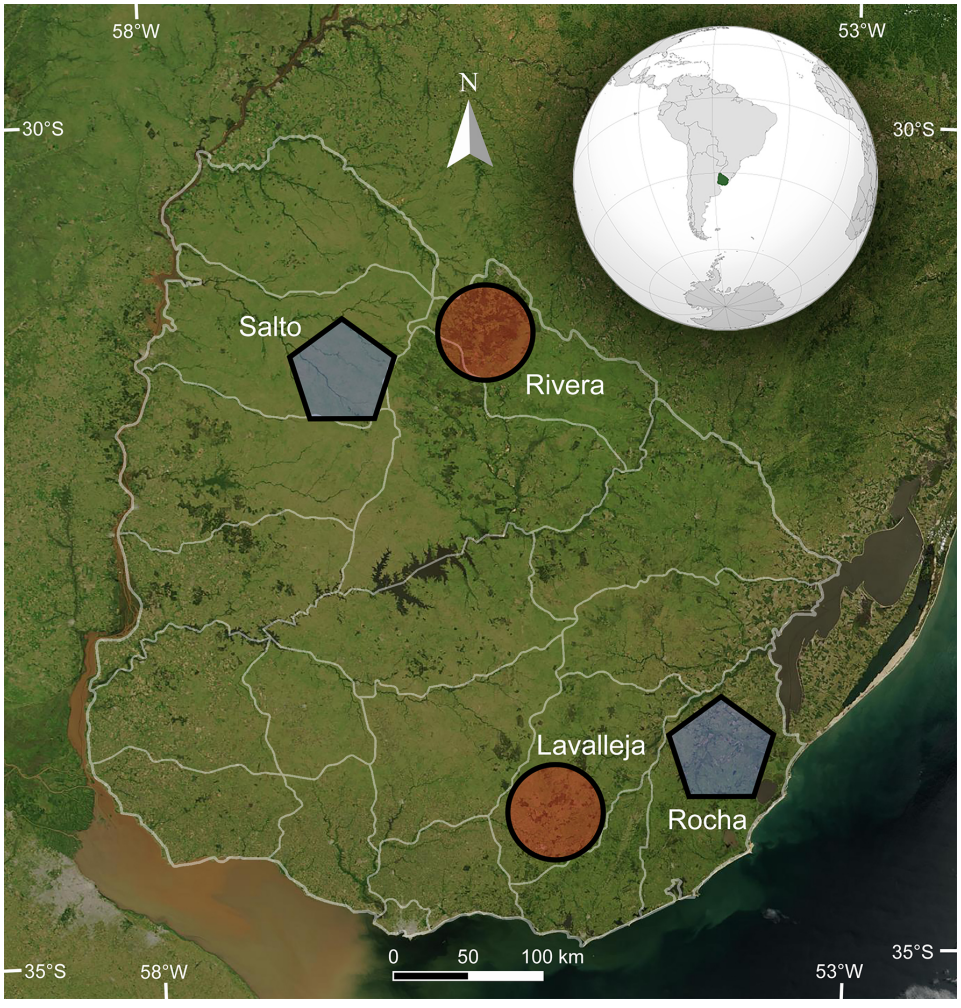

Fig. 1. Map of Uruguay showing sample collection locations. Pentagons correspond to *Ozotoceros bezoarticus*; circles correspond to *Subulo gouazoubira*. Lavalleja and Rocha correspond to the southern region. Rivera and Salto correspond to the northern region.

without accounting for subspecies or regions), the Student's t-test shows significant differences in all measurements. Specifically, *O. bezoarticus* exhibits greater values across all metrics (Supplementary Material, File S1). When comparing subspecies or regions, for *O. bezoarticus*, only GL shows significant differences, with *O. b. uruguayensis* displaying greater values than *O. b. arerunguaensis*. In the case of *S. gouazoubira*, individuals from the northern and southern regions show significant differences only in BFcr, with those from the north exhibiting the greatest values. When comparing the species in each region, in the south, *O. b. uruguayensis* exhibits significant differences from *S. gouazoubira* across all measurements. In the northern region, BFcr is the only measurement that does not show significant differences between *O. b. arerunguaensis* and *S. gouazoubira* (see Supplementary Material, File S1). When comparisons take both sex and regions into account, in *O. bezoarticus*, significant differences are observed only between males and females of *O. b. uruguayensis* individuals in GL and H measurements. Meanwhile, in *S. gouazoubira*, no significant differences are observed between males and females from the southern or northern regions (see Supplementary Material, File S1).

In the principal component analysis for *O. bezoarticus*, the sum of the first three components accounts

for 97.4% of the total variance. PC1 explains 74.1% of the variance, while PC2 and PC3 account for 17.9% and 5.4%, respectively (Supplementary Material, File S2). Along the PC1 axis, most individuals of *O. b. uruguayensis* tend to be at the positive end, while those of *O. b. arerunguaensis* are mostly at the negative end. Given this disposition, added to the fact that the factor loadings are all oriented towards the positive end and, as observed in the univariate analyses, that individuals of *O. b. uruguayensis* tend to be larger than those of *O. b. arerunguaensis*, it could be considered that PC1 is mainly related to the overall size of the element. At the same time, components 2 and 3 would be more related to the bone shape (see Supplementary Material, File S2). In this way, when analyzing PC2 and PC3, the atlas size can be taken aside and thus mainly evaluate the variation of its shape. As can be seen in **Figure** 3A, when evaluating PC2 and PC3 considering the two subspecies, there is a clear separation along PC3 between both, with the individuals of *O. b. arerunguaensis* located towards the positive end of the axis and those of *O. b. uruguayensis* towards the negative end. The factor loadings show that *O. b. arerunguaensis* are mainly differentiated by having a larger H and BFcr, while *O. b. uruguayensis* shows a larger GL. When these two components are evaluated considering sex and the region from which they come (which in this case is equivalent to subspecies), it is observed that there is an overlap between males and females in each region, prevailing the separation between subspecies (**Fig**. 3B).

For *S. gouazoubira*, the sum of the first three components accounts for 96.8% of the total variance. PC1 explains 71.9% of the variance, while PC2 and PC3 account for 18.9% and 6%, respectively (see Supplementary Material, File S2). Similarly to what is observed in *O. bezoarticus*, PC1 would be related to the overall size of the element, with individuals from the northern region being those found at the positive end of the PC1 axis and therefore being larger (see Supplementary Material, File S2). When evaluating PC2 and PC3 considering north and south regions, a separation along PC3 can be observed between northern and southern individuals (**Fig**. 3C), which is very similar to that observed in *O. bezoarticus*, with those individuals from the north located at the positive end of the component and having larger H and BFcr. In contrast, individuals from the south mainly present larger GB. When these two components are evaluated, considering sex and region, a separation is observed between males and females from each region, indicating that males tend to have higher GL than females (**Fig**. 4D). Likewise, an overlap is also observed in the morphospace occupied by males from the north with females from the southern region.

Axis

The Student's t-test shows that H is the only measurement that does not present significant differences between *O. bezoarticus* and *S. gouazoubira*. For all other measurements, *O. bezoarticus* presents greater values than *S. gouazoubira* (see Supplementary Material, File S1). However, when comparing subspecies or regions, the LAPa variable showed significant differences only in *O. bezoarticus*, with *O. b. uruguayensis* displaying greater values than *O. b. arerunguaensis*. In *S. gouazoubira*, individuals from the northern and southern regions show significant differences only in H, with those from the north having the greatest values. In both the southern and northern regions, H is the only measurement that does not show significant differences between *O. bezoarticus* and *S. gouazoubira* (see Supplementary Material, File S1). When both sex and region are considered, for *O. bezoarticus*, significant differences in H and BFcr are observed between males and females in both *O. b. uruguayensis* and *O. b. arerunguaensis*, with males having the greatest values. For *S. gouazoubira*, significant differences are only observed in BFcr between northern males and females, whereas southern males and females do not show significant differences for any of the measures. In males from both regions, the mean values of H and BFcr are larger than those of females, even though they do not reach the significance threshold (see Supplementary Material, File S1).

In the PCA for *O. bezoarticus*, the sum of the first three components accounts for 96.6% of the total variance. PC1 explains 58.6% of the variance, while PC2 and PC3 account for 32.4% and 5.6%, respectively (Supplementary Material, File S2). Since the factor loadings are all oriented towards the positive end of PC1, this component is also mainly related to the overall size of the element. Most individuals of *O. b. uruguayensis* are located at the positive end. In contrast, those of *O. b. arerunguaensis* are located at the negative one (see Supplementary Material, File S2). When evaluating PC2 and PC3 for the two subspecies, an almost total overlap of all individuals with no clear classification pattern observed (**Fig**. 4A). However, when these two components are assessed considering sex and region (or subspecies), a clear discrimination between males and females becomes evident, regardless of subspecies. Females

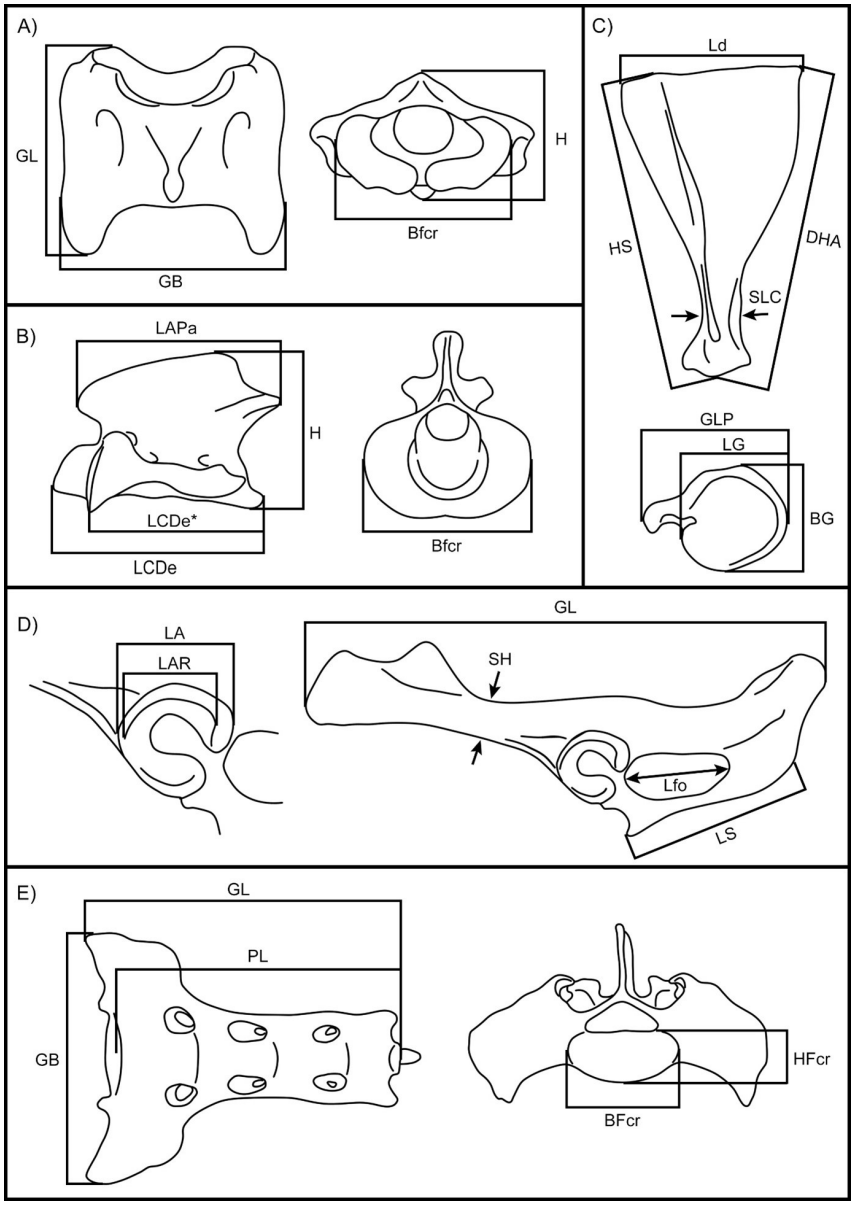

Fig. 2. Linear measurements: A) atlas; B) axis; C) scapula; D) pelvis; E) sacrum, following Von Den Driesch (1976).

from both regions share a common morphospace, distinct from males from both regions. The factor loadings indicate that males are mainly differentiated by having a greater H and BFcr, while females exhibit greater LCDe and LCDe* (**Fig**. 4B).

For *S. gouazoubira*, the sum of the first three components accounts for 97.6% of the total variance. PC1 explains 73.4% of the variance, while PC2 and PC3 account for 19.2% and 5.0%, respectively (see Supplementary Material, File S2). The factor loadings are not predominantly directed towards PC1 but rather have a strong component towards PC2, suggesting that size is not as relevant a factor in this species, which results in greater overlap between individuals from the north and south (see Supplementary Material, File S2). When evaluating

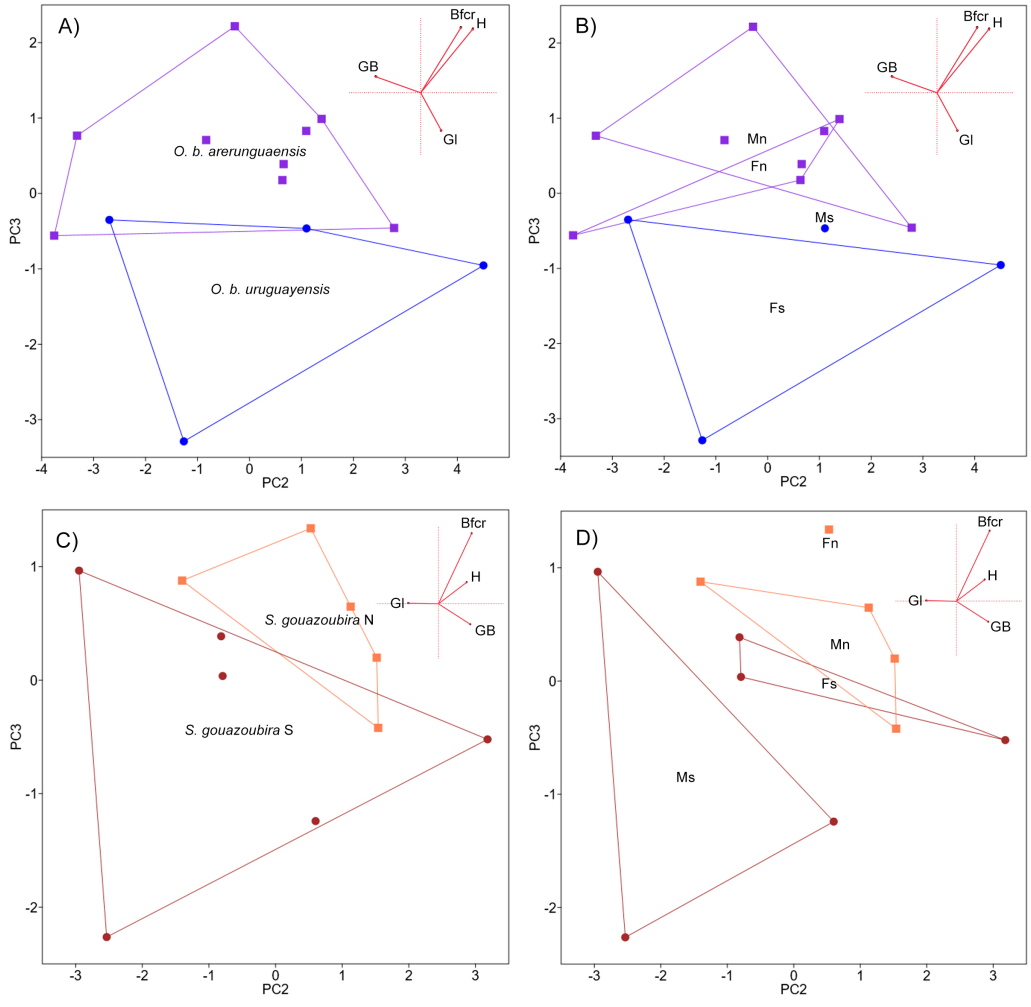

Fig. 3. Analysis of principal component 2 vs. principal component 3 for the atlas. Top, *O. bezoarticus* classified by A) subspecies and B) subspecies and sex. Bottom, *S. gouazoubira* classified by C) regions and D) regions and sex. Abbreviations: Mn, male north; Ms, male south; Fn, female north; Fs, female south.

PC2 and PC3 for the two regions, there is a complete overlap of all individuals, as in *O. bezoarticus* **Fig**. 4C). When the two components are assessed considering sex and region, a clear discrimination between males and females becomes evident, regardless of subspecies. The factor loadings indicate that males are mainly differentiated by having greater H and BFcr, while females have greater LCDe and LCDe* (**Fig**. 4D). These patterns are very similar to those observed in *O. bezoarticus*.

Scapula

In the univariate analysis, the Student's t-test shows that only SLC presents significant differences between *O. bezoarticus* and *S. gouazoubira* (see Supplementary Material, File S1). When comparing subspecies or regions within *O. bezoarticus*, most of the measurements do not show significant differences between the two subspecies. Only DHA, HS, and GLP show significant differences, with *O. b. uruguayensis* displaying greater values than *O. b. arerunguaensis* in all cases. In *S. gouazoubira*, northern and southern individuals show differences

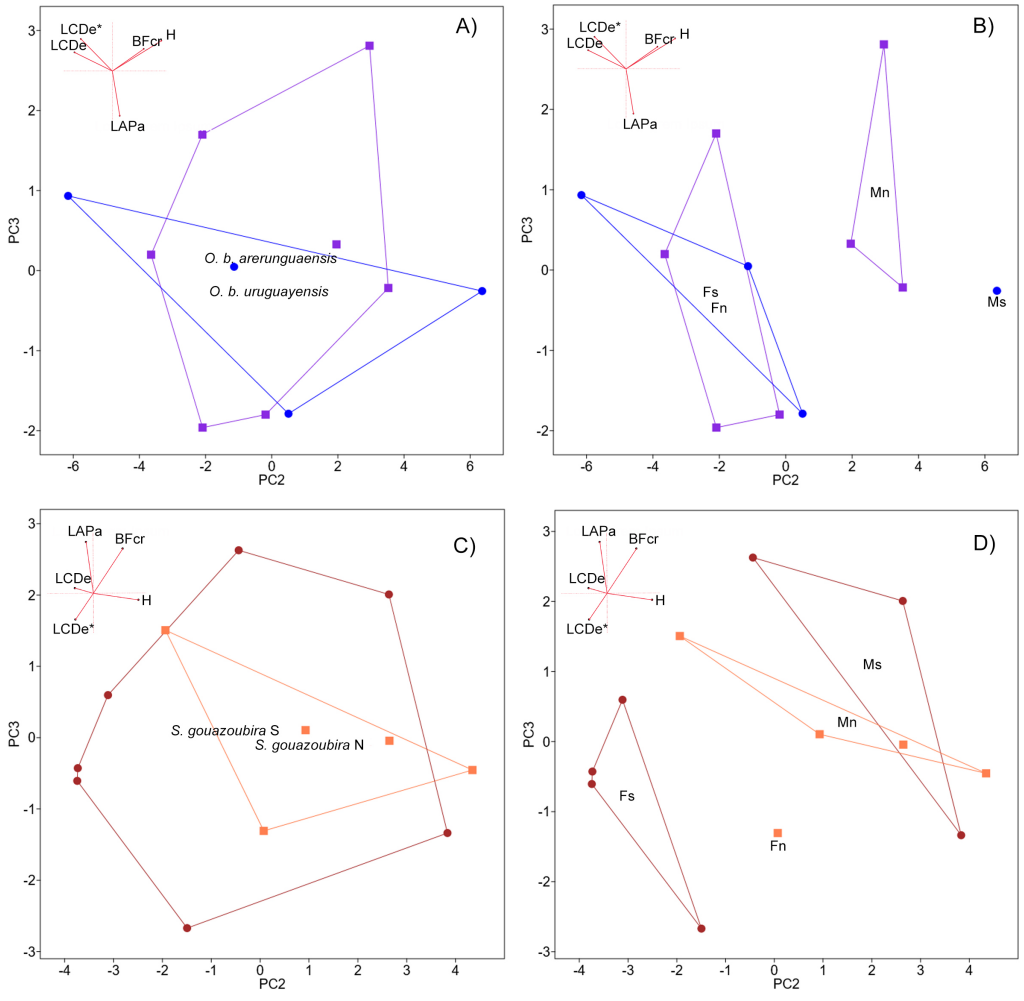

Fig. 4. Analysis of principal component 2 vs. principal component 3 for the axis. Top, *O. bezoarticus* classified by A) subspecies and B) subspecies and sex. Bottom, *S. gouazoubira* classified by C) regions and D) regions and sex. Abbreviations: Mn, male north; Ms, male south; Fn, female north; Fs, female south.

in LG, Ld, BG, and GLP, with the northern ones having the greatest values for all metrics. In the southern region, Ld is the only measurement that does not show significant differences between *O. b. uruguayensis* and *S. gouazoubira*. While in the northern region, *O. b. arerunguaensis* and *S. gouazoubira* differ significantly only in SLC and Ld (see Supplementary Material, File S1). When both sex and region are considered, in *O. bezoarticus*, none of the measurements show significant differences between male and female individuals of the same subspecies. For *S. gouazoubira*, southern individuals do not show significant differences between males and females for any of the measures. In contrast, northern individuals exhibit significant differences in LG, DHA, and HS (see Supplementary Material, File S1).

In the PCA for *O. bezoarticus*, the sum of the first three components accounts for 97.8% of the total variance. PC1 explains 87.1% of the variance, while PC2 and PC3 account for 9.0% and 1.7%, respectively (see Supplementary Material, File S2). Factor loadings are predominantly oriented towards the positive end of PC1, where most individuals of *O. b. uruguayensis* are located. Thus, this component is mainly related to overall size. Additionally, some factor loadings

Table 2

Descriptive statistics on the *Ozotoceros bezoarticus* and *Subulo gouazoubira* measurements.

Bone	Measure	*O. bezoarticus*					*S. gouazoubira*				
		n	**Min.**	**Max.**	**Mean**	**S. D.**	**n**	**Min.**	**Max.**	**Mean**	**S. D..**
Atlas	GL	13	43.7	56.8	48.3	3.74	11	34.3	43.3	39.1	2.78
	GB	13	51.6	60.3	55.7	3.20	11	47	55.7	49.3	2.80
	H	13	28	35	31.2	1.91	11	27	30.6	27.6	1.03
	BFcr	13	37.8	44.5	40.2	1.91	11	34.8	40.8	37.7	1.62
Axis	LCDe	11	51.8	60.9	54.6	2.81	12	42.6	55.4	47.8	3.32
	LCDe*	11	43.2	51.1	46.7	2.61	12	32.7	46.9	39.9	3.46
	H	11	40.8	50.8	43.4	3.02	12	36.5	49.1	41.9	3.72
	BFcr	11	33.7	40.5	36.6	1.93	12	30.8	34.8	32.6	1.07
	LAPa	11	44.9	57.4	50.7	3.38	11	39.3	46.1	42	2.51
Scapula	SLC	19	14.5	18.4	15.9	1.00	12	11.5	15.7	13.9	1.29
	Ld	18	67.1	77.8	70.7	3.23	12	65.5	82.4	71.4	5.46
	DHA	19	122.9	143.1	131.8	6.82	11	117.6	140.6	128.6	6.95
	HS	18	117.9	139.8	127.9	6.91	12	111.8	140	124.8	7.39
	GLP	19	26.1	32.6	28.4	1.62	12	25.9	30.2	27.6	1.37
	LG	19	19.4	24.5	22	1.22	12	19.6	25.2	21.4	1.52
	BG	19	18.6	23.6	20.1	1.39	12	17.4	23.2	19.7	1.69
Pelvis	GL	19	165.8	238.4	193.6	15.31	10	165.3	213.1	188	13.02
	LA	19	26.1	32.4	29.6	1.86	10	24.9	30.4	27.8	1.70
	LAR	19	19.6	27	23.3	2.05	10	19.4	23	21.5	1.09
	Lfo	19	33.6	46.9	37.5	3.21	10	32.8	41.9	37.1	2.61
	LS	19	61.1	80.7	70.4	5.50	10	58	71	66.2	3.78
	SH	19	12.3	20.5	16.7	3.75	10	14	19.2	16.9	1.84
Sacrum	GL	17	70	110	87.9	8.82	8	85.2	100.4	94.9	5.33
	GB	17	63.8	80	72.2	5.59	8	54.7	69.2	62.4	5.29
	PL	17	64	107.5	82.6	8.83	8	79	98.8	90.3	6.12
	HFcr	14	10	12.5	11.2	0.72	8	9.5	12	10.5	0.84
	BFcr	17	21.7	34	28.5	3.55	8	23.7	28.2	25.5	1.63

are strongly oriented towards the positive end of PC2, indicating that the shape of the element also plays a significant role (see Supplementary Material, File S2). When evaluating PC2 and PC3 for the two subspecies, a complete overlap of all individuals is observed, with no clear classification pattern (**Fig**. 5A). When sex and region (or subspecies) are considered, a clear discrimination between males and females is observed. The factor loadings indicate that males are mainly differentiated by having greater HS and SLC, while females have greater DHA (**Fig**. 5B).

For *S. gouazoubira*, the sum of the first three components accounts for 98.1% of the total variance. PC1 explains 81.5% of the variance, while PC2 and PC3 account for 14.3% and 2.3%, respectively (see Supplementary Material, File S2). Although factor loadings are oriented towards the positive end of PC1, a strong orientation along PC2 is also observed, with northern individuals located towards the positive end and southern ones towards the negative end, indicating a predominant role of the shape of the element in this case (see Supplementary Material, File S2). When evaluating PC2 and PC3 for the two regions, the discrimination of northern and southern individuals along PC2 remains. The factor loadings show that northern individuals mainly have greater Ld, BG, LG, and GLP, while southern individuals have greater DHA and HS (**Fig**. 5C). When sex and region are considered, the discrimination between regions remains independent of sex. That is, males from the south occupy a morphospace closer to females from the south than northern males (**Fig**. 5D).

Pelvis

In the univariate analysis, the Student's t-test shows that only LA and LAR present significant differences between both species (see Supplementary Material, File S1). When comparing subspecies or regions within *O. bezoarticus,* all measurements show significant differences, with *O. b. uruguayensis* displaying

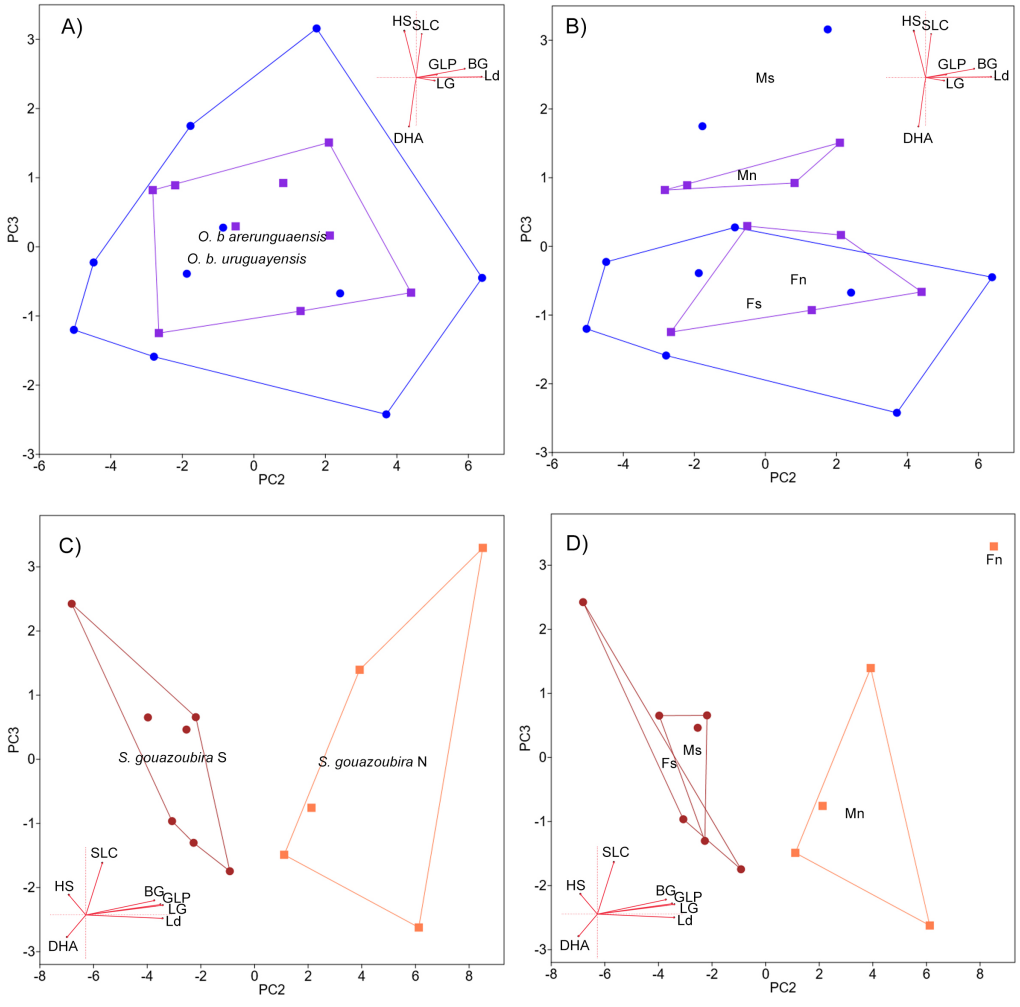

Fig. 5. Analysis of principal component 2 vs. principal component 3 for the scapula. Top, *O. bezoarticus* classified by A) subspecies and B) subspecies and sex. Bottom, *S. gouazoubira* classified by C) regions and D) regions and sex. Abbreviations: Mn, male north; Ms, male south; Fn, female north; Fs, female south.

greater values than *O. b. arerunguaensis* in all cases. In *S. gouazoubira*, significant differences are only observed in LAR and Lfo, with northern individuals having the greater values. SH is the only measurement in the southern region that does not show significant differences between *O. b. uruguayensis* and *S. gouazoubira*. In the northern region, *O. b. arerunguaensis* and *S. gouazoubira* differ significantly only in Lfo (see Supplementary Material, File S1). When both sex and region are considered, for *O. bezoarticus*, significant differences between males and females are only observed in *O. b. uruguayensis* in GL and Lfo values. For *S. gouazoubira*, no significant differences are observed between males and females for any of the measures (see Supplementary Material, File S1).

In the PCA for *O. bezoarticus*, the sum of the first three components accounts for 98.3% of the total variance. PC1 explains 91.3% of the variance, while PC2 and PC3 account for 5.5% and 1.5%, respectively (see Supplementary Material, File S2). Factor loadings are predominantly oriented towards the positive end of PC1, where most individuals of *O. b. uruguayensis* are located, indicating that this component is mainly related to the overall size of the element (see Supplementary Material, File S2). When

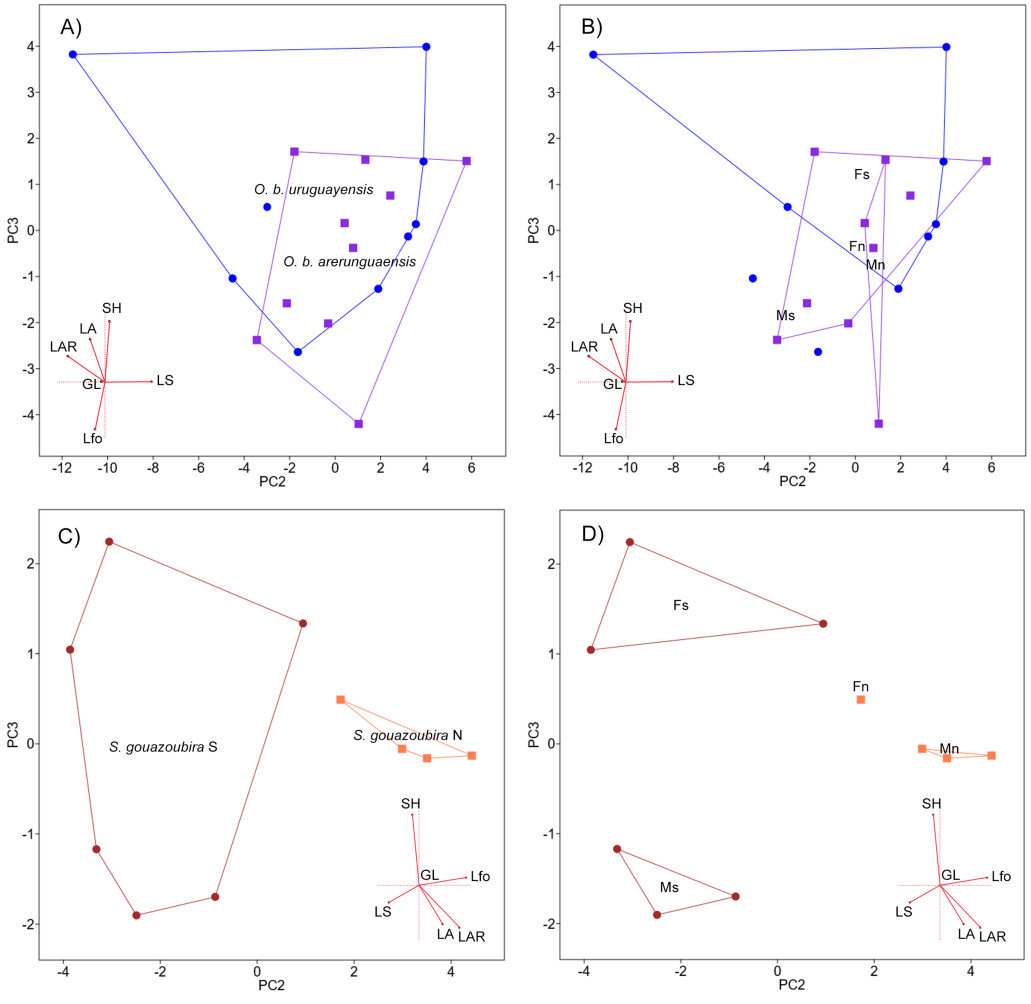

Fig. 6. Analysis of principal component 2 vs. principal component 3 for the pelvis. Top, *O. bezoarticus* classified by A) subspecies and B) subspecies and sex. Bottom, *S. gouazoubira* classified by C) regions and D) regions and sex. Abbreviations: Mn, male north; Ms, male south; Fn, female north; Fs, female south.

evaluating PC2 and PC3 for the two subspecies, there is a large overlap of most individuals, with no clear classification pattern (**Fig**. 6A). When sex and region (or subspecies) are considered, there is no clear classification pattern. However, there is a separation between males and females of *O. b. uruguayensis* along PC2, with males presenting greater Lfo and females greater SH, LA, and LAR (**Fig**. 6B).

For *S. gouazoubira*, the sum of the first three components accounts for 98.6% of the total variance. PC1 explains 93.0% of the variance, while PC2 and PC3 account for 4.7% and 0.9%, respectively (see Supplementary Material, File S2). Similar to the scapula, there is a strong orientation of factor loadings along PC2, indicating an important role of the shape, with northern individuals located towards the positive end and southern ones towards the negative end (see Supplementary Material, File S2). When evaluating PC2 and PC3 for the two regions, the discrimination between northern and southern individuals along PC2 remains. The factor loadings show that northern individuals mainly have greater Lfo, LA, and LAR, while southern individuals have greater LS (**Fig**. 6C). When considering sex and region, in addition to the regional differentiation, a clear separation between males and females is

observed, particularly among southern individuals. The factor loadings indicate that females from both regions have greater SH (**Fig**. 6D).

Sacrum

In the univariate analysis, the Student's t-test shows significant differences in all measures except GL when comparing the two species. *Ozotoceros bezoarticus* have greater values for GB, HFcr, and BFcr. In comparison, *S. gouazoubira* has greater values for PL (see Supplementary Material, File S1). When comparing subspecies or regions, within *O. bezoarticus*, there are significant differences in GB and BFcr, with *O. b. uruguayensis* displaying greater values than *O. b. arerunguaensis* in both cases. In *S. gouazoubira*, no significant differences are observed between northern and southern individuals. In the southern region, *O. b. uruguayensis* exhibits significant differences from *S. gouazoubira* in GB, HFcr, and BFcr. In the northern region, *O. b. arerunguaensis* and *S. gouazoubira* differ significantly only in GB (see Supplementary Material, File S1). When sex and region are taken into account, neither in *O. bezoarticus* nor in *S. gouazoubira* are significant differences observed between males and females (see Supplementary Material, File S1).

In the PCA for *O. bezoarticus*, the sum of the first three components accounts for 98.4% of the total variance. PC1 explains 77.1% of the variance, while PC2 and PC3 account for 18.0% and 3.3%, respectively (see Supplementary Material, File S2). Although factor loadings are oriented towards the positive end of PC1, a strong orientation along PC2 is also observed in some factors, with *O. b. uruguayensis* located towards the positive end and *O. b. arerunguaensis* toward the negative end (see Supplementary Material, File S2). When evaluating PC2 and PC3 for the two subspecies, the discrimination along PC2 remains. The factor loadings show that *O. b. uruguayensis* mainly have greater BFcr and HFcr, while *O. b. arerunguaensis* have greater PL (**Fig**. 7A). When sex and region (or subspecies) are considered, some separation between male and female individuals of *O. b. arerunguaensis* is observed, with factor loadings indicating greater GB in females (**Fig**. 7B).

For *S. gouazoubira*, the sum of the first three components accounts for 98.6% of the total variance. PC1 explains 78.3% of the variance, while PC2 and PC3 account for 17.4% and 2.9%, respectively (see Supplementary Material, File S2). It can be observed that, although the factor loadings are mainly oriented towards the positive end of PC1, there is an almost complete overlap between northern and southern individuals along both PC1 and PC2 (see Supplementary Material, File S2). When evaluating PC2 and PC3 for the two regions, the overlap between individuals from the north and those from the south remains (**Fig**. 7C). Considering sex and region, a clear separation is observed between southern males and females, with factor loadings indicating that females mainly present greater GB. In northern individuals, there is no clear difference between sexes (**Fig**. 7D). It should be clarified here that for *S. gouazoubira*, the sacral data are fewer than for other elements, which could influence the observation of the results.

DISCUSSION

This study represents the first application of osteometric analysis to discriminate postcranial skeletons of deer from Uruguay. While previous multivariate osteometric studies focused on the skull of pampas deer *O. bezoarticus* (González et al. 2002), the postcranial skeleton had not been analyzed with this methodology until now. Additionally, for gray brocket deer *S. gouazoubira*, this study stands out due to the larger sample size (12 individuals) compared to similar studies, which included only up to 4 individuals (Souza Junior et al. 2017; Loponte et al. 2019). This larger sample allows for a clearer understanding of intraspecific variability and enables more effective comparisons with other species.

The univariate analyses show that, in general, the bones of *O. bezoarticus* are larger than those of *S. gouazoubira*, with the difference particularly evident in the atlas and the axis. In the sacrum, although some measurements, such as the height and breadth of the cranial articular surface and overall width, are larger in *O. bezoarticus*, the length measurements either show no significant differences or are greater in *S. gouazoubira*. The scapula and pelvis also show no overall size differences between the two species. However, significant variation is observed in specific areas like the width of the scapular neck and the size of the acetabulum. These findings indicate that size alone is not a reliable discriminator between the two species across all bone elements.

Interestingly, these observations differ from the results reported by Loponte et al. (2019) for *O. bezoarticus* and *S. gouazoubira* in the lower Paraná region. In their study, gray brocket deer from Paraná were smaller than pampas deer. In contrast, our study found that gray brocket deer from Uruguay are larger than those from Paraná and have body sizes overlapping with those of *O. bezoarticus* from both re-

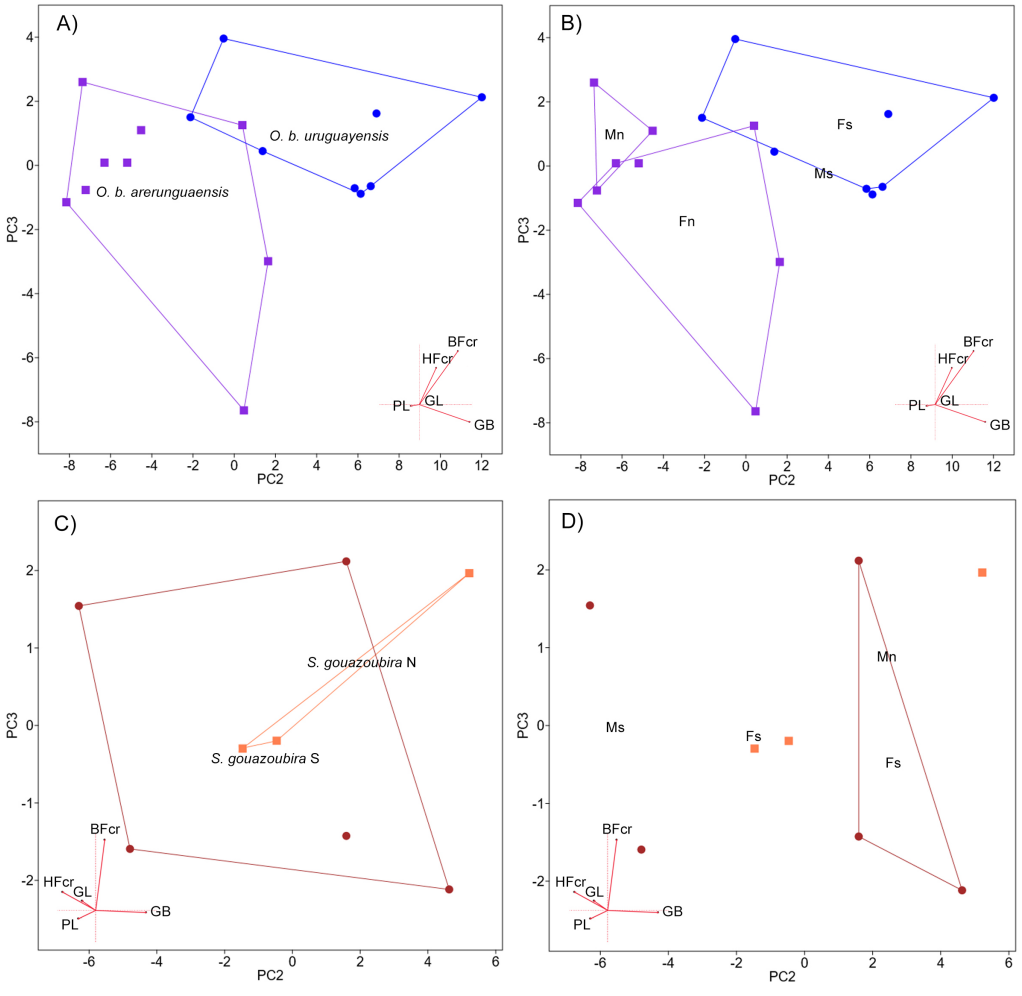

Fig. 7. Analysis of principal component 2 vs. principal component 3 for the sacrum. Top, *O. bezoarticus* classified by A) subspecies and B) subspecies and sex. Bottom, *S. gouazoubira* classified by C) regions and D) regions and sex. Abbreviations: Mn, male north; Ms, male south; Fn, female north; Fs, female south.

gions. This suggests that the size-based distinctions between species in other regions, such as Paraná, may not be applicable in Uruguay, highlighting the need for region-specific osteometric analyses in archaeological contexts.

We found significant size differences within each pampas deer subspecies. Individuals belonging to *O. b. uruguayensis* from the southeast are larger than those of *O. b. arerunguaensis* from the north, which follow the same skull trends (González et al. 2002). This pattern is consistent across almost all postcranial elements analyzed in this study.

The gray brocket deer also showed differences in size. According to Silva-Caballero & Ortega (2022), there is a latitudinal size variation, with southern individuals being larger than their northeastern counterparts. However, our findings show the opposite pattern in Uruguay, with northern individuals of *S. gouazoubira* larger than those from the southeast. This discrepancy may be explained by small-scale regional variation, as the differences observed by Silva-Caballero & Ortega (2022) were based on much larger latitudinal ranges. In any case, further research on these localized patterns is necessary to achieve a better understanding.

It is also worth noting that when comparing both species within each region. In the south, *O. b. uruguayensis* generally exhibits larger values than *S. gouazoubira* in nearly all analyzed bones. In contrast, in the northern region, the differences between *O. b. arerunguaensis* and *S. gouazoubira* are less pronounced, with a greater overlap in size. For instance, while the atlas and axis bones of *O. b. arerunguaensis* are larger, the scapula, pelvis, and sacrum show similar values or are even larger in *S. gouazoubira*. However, it is also important to consider the sexual dimorphism and how it affects discrimination between the two species. In southern individuals, the size differences mainly occur between males of *O. b. uruguayensis* and both sexes of *S. gouazoubira*. The females of *O. b. uruguayensis* show little or no distinction compared to males and females of *S. gouazoubira*. A similar pattern is observed in the northern individuals.

In pampas deer, these findings support previous studies regarding the differentiation of the two subspecies and also reveal significant differences related to sexual dimorphism. In some postcranial elements, *O. b. uruguayensis* and *O. b. arerunguaensis* show morphometric differences due to subspecies distinctions, whereas in other elements, sexual dimorphism is more pronounced. For instance, in the axis, sexual dimorphism is particularly significant, likely due to the presence of antlers in males. It has been shown that ruminants with horns or antlers exhibit significant morphological differences in cervical vertebrae due to intrasexual combat (Vander Linden & Dumont 2019). Measurements such as the width of the articular facet and the height of the spine correlate strongly with these behaviors.

Interestingly, in pampas deer, sexual dimorphism is also morphologically significant in the scapula, where it is typically less pronounced. A recent study has also demonstrated the existence of sexual dimorphism in the scapula of two Asian deer species (Kang et al. 2023). In the case of pampas deer, this dimorphism may be influenced by the development of neck musculature. For instance, muscles like the *Omotransversus* and the *Trapezius* (*pars cervicalis*), which attach to the scapula and cervical vertebrae, may account for the differences observed between males and females in certain regions of the scapula (König & Liebich 2005; Morales Muñoz et al. 2021).

Multivariate analyses reveal additional patterns not evident in univariate analyses, particularly regarding sexual dimorphism in certain elements. This is specifically true for the axis of *S. gouazoubira*. While univariate analyses showed significant sex differences only in the breadth of the cranial articular surface measurement for northern individuals, the multivariate data (PCAs) discriminate between males and females based on height and breadth of the cranial articular surface values, similar to *O. bezoarticus*. A similar pattern is observed in the scapula of *O. bezoarticus*, where multivariate analyses reveal differences between males and females not fully captured by univariate analyses.

Despite the absence of large, branched antlers in *S. gouazoubira*, significant sexual dimorphism is still observed in the axis, likely due to the use of stab-combat strategies similar to some bovids with small horns (Vander Linden & Dumont 2019). Although these fights generate less force on the neck than wrestling or ramming, they may still cause observable differences between males and females. Additionally, in *S. gouazoubira*, the pelvis and sacrum show morphometric differences attributed to sexual dimorphism, with the pelvis also displaying regional variation. In contrast, in *O. bezoarticus*, the pelvis and sacrum exhibit differences primarily due to subspecies variation rather than sexual dimorphism. While some dimorphic variation is observed within each subspecies, it is not as pronounced when all specimens are considered together, as seen in other skeletal elements like the atlas, axis, and scapula.

The osteometric differences observed between the bones of *O. bezoarticus* and *S. gouazoubira* could generally be attributed to the different habitats of each species. As previously mentioned, *O. bezoarticus* inhabits open grassy environments, while *S. gouazoubira* is primarily found in closed environments. These habitat differences may affect the size, proportions, and shape of various skeletal elements. Ecomorphological studies have shown that, in open environments, cervids rely on swift flight, and their morphological adaptations reflect rapid movement and joint stability. Conversely, cervids in closed environments must navigate a more complex, three-dimensional landscape, and their morphology reflects the need for greater mobility (Curran 2015). However, because these characteristics are primarily related to locomotion, they are more clearly observed in the limbs, which is where most ecomorphological analyses have focused, both in artiodactyls in general and in deer in particular (e.g., Plummer et al. 2008; Curran 2012, 2015; Barr 2014; Dunn & Avery 2021; Gruwier & Kovarovic 2022.

In this study, while we observed that the primary difference between the two species is generally due to the size of the elements, our focus on the axial skeleton and the girdles may have masked potential

differences related to ecomorphology. These may be overshadowed by intraspecific sexual dimorphism or differentiation between subspecies or populations, as observed in the axis, scapula, and pelvis. Future studies focusing on limb analysis will allow for a more thorough consideration of these ecomorphological adaptations, which have already proven to be significant.

Morphometric differences between *S. gouazoubira* individuals from the north and south are also significant, particularly in the atlas and the axis, which closely resemble those seen in *O. bezoarticus* between the two subspecies. However, in the scapula, sexual dimorphism predominates over regional differentiation in *O. bezoarticus*, while in *S. gouazoubira*, regional differences are more prominent. These results may indicate that *S. gouazoubira* individuals from the north form a distinct unit from those in the south, corroborating previous molecular findings (González et al. 2020).

Both the postcranial osteometric results presented here, as well as the morphometric analyses of the pampas deer skull (González et al. 2002) and previous studies on pampas deer and grey brocket deer (González et al. 1998, 2002) showing significant genetic and morphological differentiation provide evidence of a north-south regionalization that cannot be explained by a natural barrier until at least 300 years ago (Márquez et al. 2006). This differentiation may be due to deeper historical causes, possibly related to large-scale environmental changes.

During the Late Pleistocene, the paleoenvironmental conditions in northern and southern Uruguay showed some differences. The northern region is characterized by the presence of sediments from the Sopas Formation, which, given its fossil vertebrate association, suggests a heterogeneity of environments, including riparian forest, semi-open forest, and open areas, with the possible occurrence of arid and semi-arid microenvironments that may have acted as environmental refuges (Ubilla & Martínez 2016).

In contrast, the southern region is characterized by sediments from the Dolores Formation, associated with a cold and arid to semi-arid climate, featuring open to semi-open environments with a predominance of grasslands (Ubilla & Martínez 2016). However, there are also indications of more humid and closed environments (Varela et al. 2023). Paleoecological studies of the megafauna in the Río de la Plata region suggest that this area could represent an ecotone between southern and northern ecoregions, where taxa from both regions could coexist, along with the occurrence of endemic taxa with more restricted distribution limits (Varela et al. 2018). Therefore, these historical contingencies may be influencing the regionalization observed in the native deer of Uruguay.

CONCLUSIONS AND PERSPECTIVES

This study has proved that osteometry is a valid tool for discriminating postcranial osteology of two Neotropical cervids, *Ozotoceros bezoarticus*, and *Subulo gouazoubira*. The comparative approach using both univariate and multivariate statistical tools effectively identified variables that discriminate species based on taxonomy, geography, and sex. These results have enabled the identification of key discriminant variables between the two species, confirmed the previously recognized differences between the subspecies of pampas deer, and supported the genetic evidence for two distinct conservation units of *S. gouazoubira*, one in the north and one in the south. Regarding sexual dimorphism, the findings demonstrate that it is more pronounced in *O. bezoarticus* than in *S. gouazoubira,* and, in some cases, it may be linked to sexual structures and behaviors.

This new knowledge is also useful for solving taxonomic identification and sex determination challenges in archaeological and paleontological contexts. Since there had been no previous objective data on the osteometric differences between these deer in Uruguay, identifying them from isolated or fragmentary remains has been a persistent issue in paleobiological research. The discriminant metric variables identified in this study will improve the accuracy of taxonomic identifications and enhance our understanding of how ancient human populations utilized these species.

Ongoing research focusing on limb osteometry will complete this study and will allow for more precise differentiation between species with highly similar postcranial morphology, recognizing patterns of morphological variability, both inter- and intraspecific. These efforts will also deepen our understanding of the evolutionary processes that contributed to the diversification of the Cervidae family during the Pleistocene.

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